THE VIRGINIA JOURNAL OF SCIENCE

VOL. 11, NEW SERIES | April, 1960 | No. 2

The Genus *Ceratodrilus* Hall, (Branchiobdellidae, Obligochaeta) With The Description of A New Species

Perry C. Holt
Department of Biology, Virginia Polytechnic Institute
Blacksburg, Virginia

The majority of the species of the family Branchiobdellidae are monotonously similar in superficial appearance, but this general uniformity of external structure is occasionally departed from by some species in a most dramatic fashion. Notable in this respect among the North American branchiobdellids are such forms as *Pterodrilus alcicornus* Moore and the curiously ornamented species of *Ceratodrilus* which are the subjects of the present investigation.

These aptly named "horned worms," however, compel our attention and interest for several reasons other than their appearance. *Ceratodrilus* is endemic to a geologically interesting area and, moreover, the type species, *C. thysanosomus* from Utah, has been referred to *Cirrodrilus* Pierantoni, a genus of Japanese worms. Such a relationship, if real, would be a matter of considerable zoogeographical importance. Furthermore, the material at hand reveals the presence in the Snake River basin of a second, undescribed, species of the genus and, finally, the acquisition of a large number of specimens of both these species as the result of a collecting trip made in the summer of 1958 presents an opportunity to study the internal anatomy of these species. A phylogenetic synthesis of the family Branchiobdellidae waits in part on the completion of such anatomical studies.

Although the genus *Ceratodrilus* has been briefly and almost cursorily treated by only three authors, the history of these treatments has its points of interest. The story begins in 1905 when Pierantoni erected the genus *Cirrodrilus*, with *C. cirratus* as the only species, on the basis of several ill-preserved individuals which were obtained from specimens of the Japanese crayfish *Cambaroides japonicus* possessed by the Museum de Histoire Naturelle de Paris. Pierantoni's diagnosis (according to Yamaguchi, 1932a: 364) appears to have been based primarily upon what he believed to be ventrally placed transverse ridges bearing finger-like projections. In 1914, Hall diagnosed the genus *Ceratodrilus,* designating *C. thysanosomus* as the type species, on the basis of material from the Great Salt Lake basin in Utah which was likewise admitted to be in a state of poor preservation. Yamaguchi (1932a) studied some Japanese branchiobdellids and referred worms which he considered to be conspecific with Pierantoni's animals to Hall's genus *Ceratodrilus,* ignoring the priority of *Cirrodrilus* as a generic name. This assignment was based on Yamaguchi's undoubtedly correct view that Pierantoni confused the dorsal with the ventral surface of his worms and upon Hall's description of the dorsal projections of *Ceratodrilus.* Goodnight (1940: 63-64) reviewed the work of Hall and Yamaguchi, concurred with Yamaguchi's view that the American and Japanese species are congeneric and corrected Yamaguchi's violation of the law of priority, thereby reducing Hall's genus *Ceratodrilus* to synonymy.

It is immediately obvious that both Pierantoni and Hall based the diagnosis of their genera upon the external appearance of poorly preserved material; that Yamaguchi had no opportunity to study American material and made his decision to synonymize the Japanese and American genera on the basis of external form; that Goodnight simply accepted Yamaguchi's conclusions and assigned his material from the Snake River basin in Idaho and Oregon to Hall's species without considering whether these Snake River animals might represent a species other than Hall's Utah one. Goodnight did not study the internal anatomy of his animals and, hence, made no attempt to determine whether they, or Hall's, correspond to Yamaguchi's in this respect. They do not, as this investigation shows.

One objective of this paper is to establish the generic distinctiveness of the American worms and, hence, to revive Hall's genus *Ceratodrilus.* Since Japanese material is not available in America, the validity of this effort depends upon a careful interpretation of Yamaguchi's descriptions and figures. Without attempting to follow the changes in Yamaguchi's papers (1932a, 1932b, 1933, 1934), attention is directed to what appear to be his final conclusions as found in his monograph of the Japanese branchiobdellids (1934). Here he again ignored priority and placed the Japanese species *Cirrodrilus cirratus* in Pierantoni's genus *Stephanodrilus.* If Yamaguchi was correct in believing that Pierantoni's *Cirrodrilus cirratus* (1905) and *Stephanodrilus sapporensis* (1906) are congeneric, then *Stephanodrilus,* not *Cirrodrilus,* becomes a junior synonym. But this is not important to the present argument. What is important is that Yamaguchi considered the species of *Cirrodrilus* and *Stephanodrilus* to be congeneric and his concept of the genus, which, if he and Goodnight were correct, would embrace the American species upon which Hall erected his genus *Ceratodrilus*.

Consequently, Yamaguchi's concept of the genus *Stephanodrilus* must be considered. The pertinent point is that Yamaguchi understood the structure of the male reproductive system of the branchiobdellids, including the American genus *Cambarincola* which has an introduced representative in Japan (1934: 191). He wrote (1934: 190-191) that the latter has an accessory sperm tube (=prostate, see below). In his paper on what he then called *Cambarincola homodonta* (1932c: fig 2) a species he later placed in *Stephanodrilus* (1934: 200-201), he presented drawings of the spermatic vesicles (=spermiducal glands, see below) and atria (=bursae and penial sheaths, see below) of several species of branchiobdellids. These drawings clearly show that there is no prostate in *Stephanodrilus sapporensis* and in *S. homodonta*, while his drawing of *Cambarincola sp.* shows the typical structure of the male reproductive system of this genus. The species originally called *Carcinodrilus nipponicus* was at first considered generically distinct from those assigned to *Ceratodrilus* [=*Cirrodrilus*] and *Stephanodrilus* on the basis of differences in the external form, but the statement is made (1932b: 63) that these genera are "generally similar" in internal structure. It is implicit in Yamaguchi's 1934 paper and previous work that he made his decision to assign the fairly numerous species of Japanese worms to the three genera *Branchiobdella, Cambarincola* and *Stephanodrilus* on the basis of differences in the structure of the male reproductive system. Be this as it may however, Yamaguchi gave clear enough description of the male reproductive system of the Japanese worms to establish the generic distinctiveness of the American ones.

As further evidence bearing on this point, he figured the "atrium" (=bursa, penial sheath and spermiducal gland) of *Stephanodrilus inukaii.* This drawing, reproduced here (fig. 1), is entirely consistent with his earlier ones mentioned above. The essential points to note are the absence of the prostate and the point of entry of the vasa deferentia into the spermiducal gland. He then remarked for all of the fifteen species (with the exception of Pierantoni's *Stephanodrilus japonicus* which he did not see) that the male reproductive system is generally similar and made it clear that it corresponds in all these species to the drawings he presented of *S. inukaii, S. sapporensis* and *S. homodonta.* The Japanese worms which Yamaguchi assigned to *Stephanodrilus* constitute a coherent group and are congeneric according to the generic concept adhered to in this paper.

Yamaguchi's (1934: 191-192 diagnosis of *Stephanodrilus* was somewhat long and emphasized the external features perhaps unduly. A condensed version, however, would read: peristomium always 8-lobed dorsally, the lobes often prolonged into tentacles, frequently with a membranous funnel-like extension of the peristomium between the lobes; with or without dorsal transverse bands and projections; anterior nephridiopores usually paired, unpaired in S. *koreanus* [?]; both dorsal and ventral jaws with 7 or more teeth, including always a large median one; "testes and male funnels in trunk somites V and VI; atrium of [a] glandular part, muscular portion and bursa, no distinct penis sheath; glandular atrium not bifid, [but] tubular or bulged [in] form; no paired bursal glands; penis sub-conical in form, having a narrow eversible efferent duct folded several times at the basal portion; spermatheca not bifid and composed of two enlarged portions, one in the distal [read "ental" (?)] end, the other in about the middle portion, lumen [sic] of the two portions connected by a very narrow canal."

This constitutes a coherent generic diagnosis and one would question only the unpaired nephridiopore of S. *koreanus* and the absence of a statement concerning the point of entry into the spermiducal gland (glandular atrium) of the deferent ducts. The first may simply be an error; if not, the Korean species probably represents a different genus. The latter point is important and it is clear from Yamaguchi's drawings and descriptions that the Japanese genus, properly known as *Cirrodrilus,* is characterized in part by the fact that the deferent ducts enter the spermiducal gland at a point about one-fourth the length of the gland entad from the junction of it and the ejaculatory duct (fig. 1), as in the American genus *Xironogiton* (Holt, 1949: 541) which otherwise appears to be quite distinct from the Japanese genus.

There is no reason to doubt the accuracy of Yamaguchi's observations with the exceptions noted. There are, then, two known indigenous genera of branchiobdellids, *Branchiobdella* Odier, 1823, and *Cirrodrilus* (including *Stephanodrilus*) Pierantoni, 1905, and the introduced American species of *Cambarincola* in Japan and Korea.

Goodnight (1940: 63) concurred with Yamaguchi's error in reducing the American genus *Ceratodrilus* to synonymy with the Japanese genus *Cirrodrilus.* A brief consideration of Goodnight's treatment, therefore, becomes pertinent.

Goodnight (1940: 63) defined *Cirrodrilus,* including *Ceratodrilus,* as follows: "With the characteristics of the subfamily [two pairs of testes]; spermatheca simple, not bifid; no accessory sperm tube; anterior nephridia opening to the outside through separate pores in the dorsal half of segment III; penis eversible; body cylindrical, not depressed; with body appendages in the form of pointed bands extending transversely across the dorsal surface." His discussion of the genus was short and consisted of a quotation from Yamaguchi justifying the combining of the genera on the basis of Pierantoni's error. Goodnight, then, left the matter precisely at the point reached by Yamaguchi, except for his correction of Yamaguchi's error in regard to priority.

MATERIALS AND METHODS

Materials collected and preserved in alcohol-formalin (70% alcohol, 96 parts; 40% formalin, 4 parts) were studied by means of whole mounts and serial sections. Animals mounted entire were dehydrated with alcohol, cleared in clove oil and mounted unstained in balsam. Sections, cut at 10 microns, were stained with Delafield's hematoxylin and eosin according to the usual procedures. Entire animals were studied with a fluorite oil immersion objective, 40X, N.A. 100, corrected to a working distance of 1.5 mm., and sections with an apochromatic, 47.5X, N.A. 0.95 objective and an apochromatic, 90X, N.A. 1.30 oil immersion objective. All drawings were made with the aid of a camera lucida. Specimens cited which are in the collections of the author are identified by the initials PCH.

I am grateful to Dr. Horton H. Hobbs, Jr., of the University of Virginia, for material collected by Tracey from Lincoln County, Wyoming, and by D. Eldon Beck from Bear Lake County, Idaho, as well as for all identifications of the host crayfish. Mr. Richard L. Hoffman aided in the preparation of materials and carefully read the manuscript. The assistance of Ray Bronson and Judson Ford in collecting crayfish in a strange desert country is gratefully acknowledged.

The work reported here was done with the aid of a grant (NSF-G4439) from the National Science Foundation.

Ceratodrilus Hall, 1914

Ceratodrilus, Hall, 1914: 190-191; *Ceratodrilus,* Stephenson, 1930: 901; *Cirrodrilus,* Goodnight, 1940: 63-64.

DIAGNOSIS. – Medium sized worms, 3.0 to 3.3 mm. in average length for the known species; finger-like projections borne on the dorsal surface of segments ii-vii; peristomium with four tentacles; a single anterior nephridiopore, opening mid-dorsally on the transverse ridge of segment iii; jaws relatively heavy, brown, teeth subequal in length, dental formula 7/6; prostate reduced to a lateral prostatic bulb near the ental end of the spermiducal gland; spermiducal gland prominent, deferent ducts enter its ental end; ejaculatory duct present, short and thick; penial sheath relatively short and thick, enclosing an eversible penis, externally only slightly delimited from the atrial portion of the bursa; spermatheca with a wide and prominent ectal stalk and an ental process.

TYPE SPECIES. — *Ceratodrilus thysanosomus* Hall, 1914, by original designation.

DISTRIBUTION. — The species of *Ceratodrilus* seem to be confined to the Snake River drainage and its Pleistocene extension into Lake Bonneville (fig 2). Hall's original material came from "streams of Great Basin, Salt Lake City, Utah," and Goodnight's subsequent records should, with the exception of the animals from Evanston (Bear River), Wyoming, be assigned to the new species described below. That the animals from the Snake River and its tributaries are specifically distinct from those of the Great Salt Lake drainage and that the genus is known only from these two formerly connected drainage systems may imply the post-Pleistocene differentiation of these species.

AFFINITES OF THE GENUS CERATODRILUS. — The Plylogenetic relationships of the branchiobdellid genera are not known and a discussion of the affinities of *Ceratodrilus* is further complicated by the fact that several unnamed genera are known. The preponderance of morphological evidence indicates that *Ceratodrilus* is more closely related to such American genera as *Cambarincola* and *Pterodrilus* and perhaps most closely of all to one of the undescribed genera in the author's collections. No genus of branchiobdellids is known with certainty to range over more than one continent — Pierantoni's (1912: 14, 16) report of the presence of *Branchiobdella* in America remains unconfirmed and the Japanese species assigned to the genus may well represent a new genus of the subfamily Branchiobdellinae. It begins to appear, therefore, that there are two, and perhaps three distinct faunal assemblages of these worms.

A further comparison of *Ceratodrilus* with the known genera of branchiobdellids is given below in conjunction with a discussion of the anatomy of the genus.

Ceratodrilus thysanosomus Hall, 1914

(Plate III, figs. 11 and 12)

Ceratodrilus thysanosomus, Hall, 1914: 191; *Ceratodrilus thysanosomus* Stephenson, 1930:801; *Ceratodrilus thysanosomus,* Yamaguchi, 1932a: 367; *Cirrodrilus thysanosomus,* Goodnight, 1940: 64-65 (in part).

DIAGNOSIS. — About 3.2 mm. in length (preserved material); head with 4 tentacles which average approximately 90 microns in length; transverse dorsal ridges bearing 4-6 finger-like projections on segments ii-vii, about 50 microns in length; segment viii with 7-8 such projections which are somewhat shorter; dorsal projections approximately 1/10 body diameter in length; spermiducal gland large, reaching almost to dorsal border of segment vi; prostate reduced to prostatic bulb which opens directly into the lumen of the spermiducal gland near the ental end.

DISCUSSION. — Hall (1914: 191) described his animals upon which the original species diagnosis was based as 2 to 2.8 mm. in length with a maximum head diameter of 400 microns, a maximum body diameter of 660 microns, a maximum sucker diameter of 360 microns and a maximum length of the tentacles of the head of about 180 microns. In his generic diagnosis based on this species, he said that the lobes of the peristomium are provided with 4 or 5 papillae each; "the first seven trunk segments are furnished with dorsal appendages extending from the lateral border in a pointed band, the number of points usually 6, but on some segments 7 or 8 . . . penis eversible."

The specimens upon which this study is based are apparently larger than Hall's (table 1). All the measurements which follow are of ten mature specimens selected for mounting and hence larger than the average for the entire series. The average is given first, followed by the range in parentheses for these ten specimens. The body length is 3.2 mm. (3.0-3.6 mm.). This difference between these animals and Hall's is almost surely of no importance. The head diameter of the animals studied is .32 mm. (.31-.40 mm.); the diameter of segment vi is .49 mm. (.39-.55 mm.); sucker diameter is .31 mm. (.29-.35 mm.); the tentacles are .09 mm. (.06-.11 mm.). No conclusions can be drawn by the comparison of these measurements with those made by Hall except that within somewhat wide limits they are similar and there is almost surely a degree of overlapping in all of them.

The oral papillae of specimens studied (fig. 4) number 14-16. It is difficult to count them, and one cannot be sure of the exact number in any case. The difference between Hall's and the author's counts are almost certainly due to this difficulty.

Hall's statement that the dorsal projections are on segments i to vii ("the first seven trunk segments") is erroneous; his illustration shows clearly the first row of projections on segment ii. More importance should be attached to the statement that there are "usually 6" dorsal projections in each row. There are 8 projections on segment viii of the material studied as is apparently the case for Hall's, and the other projection bearing segments have four, sometimes five. There is some variability in this character and only more collecting can determine whether these differences constitute a specific or subspecific difference or whether they are simply an expression of intra-specific variability. Since the author's collection was taken from a region within the type locality of Hall's species and there is doubt about all detectable differences, these specimens are assigned to *C. thysanosomus.*

The penis of these animals is eversible as Hall states is true of his. A fuller description of the reproductive systems and other points not mentioned by Hall is presented below.

TYPE LOCALITY.—Streams of Great Basin, Salt Lake City, Utah (Hall, 1914: 191).

ADDITIONAL LOCALITY RECORDS. — Evanston, Bear River, Wyoming, (Goodnight, 1940:65), on *Pacifastacus gambelii* (Girard). This is in the Great Salt Lake drainage and the record is probably valid.

Paris, Idaho. Host: *P. g. gambelii.* Oct. 28, 1950. Collector: D. Eldon Beck (PCH 424, U.S. Nat. Mus. No. 29916).

Brigham City, Box Elder County, Utah, two miles east of Brigham City on U.S. Highways 89 and 91. On *P. g. gambelii* taken from a cold, rocky, medium sized stream of the Wasatch Mountains, July 13, 1958. Collectors: P. C. and V. F. Holt (PCH 781, U. S. Nat. Mus. No. 29915).

DISPOSITION OF MATERIALS.—Type specimens: Cat. No. 17708, U. S. Nat. Mus. (Bureau of Animal Industry Helminthological Collection) (Hall, 1914: 191).

Material upon which this study is based consists of several specimens mounted entire, U.S. Nat. Mus. Nos. 29915 and 29916, and numerous specimens, including serially sectioned ones, in the author's collection (PCH 424 and 781).

Ceratodrilus orphiorhysis, n. sp.

(Plate IV, figs. 13-16)

DIAGNOSIS.—About 3.0 mm. in length (preserved material); head with 4 tentacles which average 200 microns in length; with 6 dorsal projections averaging 146 microns in length on segments ii to vii; segment viii with 8 projections which average 94 microns in length; dorsal projections approximately 1/4 body diameter in length; spermiducal gland extending dorsad about 2/3 the diameter of the segment; prostate consisting of a larger and more obvious prostatic bulb than that of *C. thysanosomus*, emptying into the lumen of the spermiducal gland near the ental end.

DISCUSSION.—*C. ophiorhysis* is closely related to *C. thysanosomus*. Externally, these species differ strikingly in appearance; a difference almost, if not entirely, due to differences in proportion. The general similarity of internal structures revealed by a study of prepared material is somewhat surprising. A more detailed account of the anatomy of both species is given here in the following section.

C. ophiorhysis has been taken at several localities in the Snake River. Goodnight's (1940:65) records of *C. thysanosomus* from Idaho and Oregon are here assigned to *C. ophiorhysis* on the basis of this distribution.

TYPE LOCALITY—Snake River, between Buhl and Wendel, Gooding County, Idaho. Host: *Pacifastacus gambelii connectans* (Faxon). July 14. 1958. Collectors: P. C. and V. F. Holt and Judson Ford (PCH 786).

ADDITIONAL LOCALITY RECORDS.—Burley, Cassia Co., Idaho, (Goodnight, 1940: 65) on *P. gambelii.*

"Bvous" [=Burns], Harney County, Silver River, Oregon (Goodnight, 1940: 65), on *P. gambelii.*

Crow Creek, South River, Lincoln County, Wyoming. Host *P. g. gambelii.* Sept. 14, 1946. Collector: Tracey, (PCH 420).

Shoshone Falls, Jerome County, Idaho. Host: *P. g. connectans.* June 15, 1928. Collector: D. Eldon Beck (PCH 423).

Bridge, Cassia County, Idaho. From Raft River on county road between Bridge and Almo. Host: *P. g. gambelii.* July 13, 1958. Collectors: P. C. and V. F. Holt and Ray Bronson (PCH 782; U.S. Nat. Mus. No. 29913).

Hagerman, Gooding County, Idaho. Cold spring in Snake River Canyon. Host: *P. g. gambelii x g. connectans.* Collectors: P. C. and V. F. Holt and Judson Ford (PCH 784; U.S. Nat. Mus. No. 29912).

Idaho Fish Hatchery, Riley Creek, Gooding County, Idaho. From head race of fish hatchery. Host: *P. g. connectans.* July 14, 1958. Collectors: P. C. and V. F. Holt and Judson Ford (PCH 785; U.S. Nat. Mus. No. 29914).

DISPOSITION OF MATERIAL.—The holotype, U. S. Nat. Mus. No. 29910, and four paratypes, U.S. Nat. Mus. No. 29911 and those noted above, are deposited in the United States National Museum. Three paratypes and the numerous remaining specimens are retained in the author's collection.

REMARKS ON THE ANATOMY OF *Ceratodrilus*

A genus based on two closely related species, one newly described, should be subjected to a careful anatomical study. The proper placing of any subsequently discovered allied species and an understanding of the evolution of the family depend on such studies.

A minor task, however, takes precedence. The nomenclature applied to the various parts of the reproductive systems of the branchiobdellids is in a state of confusion and this opportunity is taken to define terms that will be used in the future for these structures. No implications of homology should be understood, though an effort has been made to use terms that apply to structures which, if not homologous throughout the Oligochaeta, are at least analogous and generally similar in structure. References are made to Stephenson (1930) where applicable; new usages are italicized.

TERMS APPLIED TO THE MALE REPRODUCTIVE SYSTEM.—1.Testis. The testes of the branchiobdellids are paired proliferations of the posterior faces of septa 4/5 and 5/6, or 4/5 only, and are not patent in the adults of any described species known to the author.

2. Morula. A morula is a group of spermatogonia or spermatocytes. The testis at maturity breaks up, releasing the morulae which with the resulting spermatozoa fill the coeloms of segments v and vi, or v in the case of *Branchiobdella* which has only one pair of testes (Stephenson, 1930:443).

3. Blastophore. A blastophore consists of the residual cytoplasm of a morula (Stephenson, 1930:446).

4. Male funnels. Openings of efferent ducts into the coeloms of the testicular segments through which spermatozoa enter the male efferent system, common to all oligochaetes, are generally called the male funnels. A pair of funnels are located in the posterior ventral portion of each testicular coelom.

5. Efferent ducts (vasa efferentia). The male funnels open into the efferent ducts which in turn unite ventrally to form a deferent duct for each testicular segment.

6. Deferent ducts (vasa deferentia). The deferent ducts course in the ventral body wall and then freely in the coelom of segment vi where they

unite to form the spermiducal gland.

7. Spermiducal gland. In the usage of Beddard (Stephenson, 1930: 357), spermiducal glands are any glands associated with the male system. Here the term is restricted to a glandular organ formed by the union of the deferent ducts—the glandular "spermatic vesicle" of Moore (1895: 520) and the "glandular atrium" of various authors.

8. Prostate. A term used for various types of glands associated, usually directly, with the male reproductive system of the oligochaetes; it is here applied to the structure called the "accessory sperm tube" by Ellis (1912: 483). The prostate opens into the spermiducal gland, or the two unite at the point where the spermiducal gland becomes muscular to form the ejaculatory duct, and ends blindly entally. Histologically, the prostate may be similar to or different from the spermiducal gland.

9. *Prostatic bulb.* The prostatic bulb is a bulb-like structure composing the ental closed end of the prostate. It is formed of flattened, nonglandular cells and is not present in all species.

10. Ejaculatory duct (Holt, 1949:542). The ejaculatory duct is a muscular portion of the male reproductive system between the spermiducal gland and the penis formed by its ectal end. It was called the muscular sperm sac by Moore (1895: 521).

11. Bursa. The ectal muscular portion of the male reproductive system is usually called the bursa. The following portions of this organ are here recognized: a. penial sheath (Moore, 1895: 521). The penial sheath is a muscular investment of the protrusible or eversible portion of the ejaculatory duct which forms the penis and is similar to the "atrial sac" described by Benham and called the penial sac by Stephenson (1930: 348). b. penis. The protrusible or eversible, possibly intromittent, ectal portion of the ejaculatory duct is known as the penis. c. atrium. The atrium is a sac-like invagination of the body wall forming a cavity into which the penis opens when withdrawn. The muscular wall of the atrium is continuous with the penial sheath and is eversible in most, not all, genera of the branchiobdellids.

12. Male pore. The outlet pore of the bursa through which the penis everts or is protruded is generally referred to as the male pore.

TERMS APPLIED TO THE FEMALE REPRODUCTIVE SYSTEM.—The ovaries and ovipores constitute the primary female organs of the branchiobdellids. They are located in segment vii. The unpaired spermatheca of segment v varies enough in structure to justify the introduction of a few descriptive terms.

1. *Spermathecal bursa.* An invagination of the body wall surrounding the outlet pore of the spermatheca is here recognized and named the spermathecal bursa. In some species it may be eversible.

2. Spermathecal duct. The spermathecal duct is a glandulo-muscular part of the spermatheca which does not normally store spermatozoa (Holt, 1955: 29).

3. *Median duct.* Usually absent, the median duct is a narrowed region which connects the enlarged spermathecal duct of some species and the spermathecal bulb.

4. Spermathecal bulb. The spermathecal bulb is a thin walled portion of the spermatheca, usually expanded, serving for the storage of spermatozoa and sometimes glandular in structure (Holt, 1955: 29).

5. *Ental process.* The ental process is a narrowed, glandular, ental projection of the spermathecal bulb.

BODY SHAPE AND SIZE.—The general appearance of the worms treated in this paper is best presented visually (figs. 4, 11 and 13). The mea-

Table 1. A comparison of *Ceratodrilus thysanosomus* and of *C. ophiorhysis* with respect to six characters. (all measurements are in millimeters and are based on ten animals.)

	C. thysanosomus		*C. ophiorhysis*	
	Average	Range	Average	Range
Head				
length	.47	.45-.51	.47	.40-.51
diameter	.32	.31-.34	.33	.28-.37
Body				
length[1]	2.76	2.57-3.08	2.52	2.01-2.80
Diameter				
Segment i	.30	.28-.34	.39	.24-.34
Segment vi	.49	.40-.55	.53	.40-.81
Sucker	.31	.29-.35	.36	.28-.40

[1]exclusive of head.

surements given in table 1 are comparable[1] and show that *C. ophiorhysis* apparently tends to be a slightly shorter and thicker worm. *C. thysanosomus* has proportionally much shorter dorsal projections and cephalic tentacles and the body is usually flexed to a greater extent. The result is that the subjective impression is the reverse of what the measurements show.

The most obvious differences between the two species of *Ceratodrilus* are the lengths of the cephalic tentacles and dorsal projections. The measurements presented in table 2, and a comparison of the illustrations (figs. 11 and 13), show that there is no overlap in the lengths of characters; that the tentacles and projections of *C. ophiorhysis* are consistently twice, or more, the length of those of *C. thysanosomus.*

The digestive, circulatory and nervous systems of the branchiobdellids furnish little in the way of variety of use in systematics. No attempt was made to study these systems in *Ceratodrilus.* The gut is straight and sacculated in each segment in contrast to the loops in the segment vii of

Table 2. A comparison of lengths of the dorsal projections of segments ii, iv, vi, viii and of the cephalic tentacles of *Ceratodrilus thysanosomus* and *C. ophiorhysis.* (the figures are given in microns and are based on ten animals of each species selected at random and mounted entire in balsam.)

	C. thysanosomus		*C. ophiorhysis*	
	Average	Range	Average	Range
Dorsal Projections of Segments				
ii	53	24-95	176	119-254
iv	52	32-80	146	119-198
vi	44	24-64	115	87-151
viii	44	32-56	94	71-111
Cephalic Tentacles	88	56-111	201	135-278

[1] The animals were collected on successive days. Ten, randomly selected for mounting entire, were measured.

Xironogiton, and empties dorsally through the anus on segment ix.

Oral papillae have been mentioned by a few authors other than Hall. Yamaguchi (1934:195) remarked that there are sixteen for one of his species. No one seems to have determined whether or not the numbers of these structures vary among the branchiobdellids. There appear to be (fig. 4) sixteen in *Ceratodrilus ophiorhysis.*

JAWS. — The jaws of the branchiobdellids are cuticular thickenings of the posterior pharyngeal region located presumably in the posterior part of the first cephalic segment (the segmentation of the "head" of the branchiobdellids is not entirely clear). The size, shape and general appearance of these structures seem to be similar for groups of species, hence of some importance as generic characters. Those of the species of *Ceratodrilus* are relatively heavy, dark in color, crescentic in dorsal or ventral views (figs. 15 and 16), triangular in lateral view and essentially rectangular in frontal view. The dorsal jaw bears seven teeth; the ventral, six. Hall's (1914: 191) illustrations show the frontal aspect of the jaws of *Ceratodrilus thyanosomus* quite well. The jaws of the species of *Cirrodrilus* are markedly triangular in frontal aspect and those of *Ceratodrilus* are not closely similar to those of any branchiobdellids known to the author.

NEPHRIDIOPORE. Hall (1914: 191) was unable to determine whether the anterior nephridia of *C. thysanosomus* have a common opening or separate ones. Yamaguchi in his diagnosis of *Stephanodrilus* [= *Cirrodrilus*] said that there are paired ones in this genus. Goodnight (1940:63) apparently accepted this condition as true of *Ceratodrilus* when he concurred with Yamaguchi's opinion that these genera should be united. As remarked above, the nephridia of *Ceratodrilus* open to the outside through a common pore located mid-dorsally on the transverse ridge of segment iii (fig. 9). The outlet ducts of the nephridia enter the body wall laterally and course dorsad between the longitudinal and circular muscles. At the point of junction of these two ducts there is a slight dilation. Associated with this junction are a few cells which take a deeper basic stain than do those of the nephridial ducts and are apparently glandular in nature. The common outlet duct is quite short, the lumen is essentially collapsed and the nephridiopore itself is not raised above the surrounding part of the dorsal ridge. A common nephridiopore is characteristic of the genera *Cambarincola* Ellis, *Bdellodrilus* Moore and *Pterodrilus* Moore.

THE MALE REPRODUCTIVE SYSTEM. The anatomical studies reported here concern structures which vary from one group of branchiodbellids to another and are, therefore, of importance in systematic studies. The various parts of the male reproductive system differ somewhat in size

Table 3. A comparison of selected dimensions of the reproductive organs of *Ceratodrilus thysanosomus* and *C. ophiorhysis.* (the figures are given in Microns and are based on ten animals of each species, selected at random and mounted entire in balsam.)

	C. thysanosomus		*C. ophiorhysis*	
	Average	Range	Average	Range
Length of Bursa	286	244-339	300	260-331
Diameter of Bursa	154	118-173	157	118-181
Length of Spermiducal Gland	318	276-434	283	237-355
Diameter of Spermiducal Gland	111	94-118	89	79-94
Diameter of Spermathecal Duct	120	111-142	102	79-118
Diameter of Spermathecal Bulb	112	79-142	110	94-126

in the two species and a series of measurements of these are reported here (table 3). It is felt that ultimately such measurements, when treated statistically, may be of value in defining closely related species. *C. thysanosomus* and *C. ophiorhysis* are distinct in other respects and no attempt was made to determine the level of significance of the differences of means in the measurements reported.

The measurement of these structures is difficult, since they often lie obliquely to the horizontal plane. Those for the diameter of a cylindrical organ are felt to be somewhat more reliable than the others. The bursae of the two species appear to be of the same size. The spermiducal gland of *C. thysanosomus* is larger than that of *C. ophiorhysis;* a noticeable difference which accounts for the more crowded appearance of segment vi of the former species. The spermatheca of *C. thysanosomus* may also be somewhat larger than that of *C. ophiorhysis.*

Other than that both segments v and vi are testicular segments, the testes of *Ceratodrilus* are not apparent at maturity and nothing further can be said about them. The coeloms of the mature testicular segments are filled with spermatozoa. The male funnels of the branchiobdellids do differ from species to species in shape and size; those of *Ceratodrilus* flare widely and are somewhat shorter in total length than the diameter of the flared ental end. *C. ophiorhysis* may possess funnels with a somewhat wider ental end, but this subjective opinion is unconfirmed by measurements. Some variability in the location of the funnels seems to occur: in *C. thysanosomus* both funnels of a segment have been found on the same side of the segment quite close together, an arrangement of the funnels not known for any other branchiobdellid. Nothing of importance was noticed concerning the efferent and deferent ducts.

Spermiducal gland: The spermiducal gland of *Ceratodrilus* is histologically similar to that of other species of branchiobdellids (Moore, 1895: 521; Holt, 1949: 542, 552). Since the organ is composed of a glandular lining epithelium covered with a thin muscular coat and a thinner peritoneal layer, the gland cells are very tall columnar cells with basal nuclei. They contain droplets of secretory material towards their outer ends (fig. 10). Occasionally, there are cilia present projecting into the lumen of the gland (one specimen of *C. ophiorhysis*), but apparently this is not characteristic. Always there is a meshwork of secreted material in the lumen of the gland.

The deferent ducts enter the gland at its ental end and in *C. thysansomus* the gland is indented, not as much as in some species of *Cambarincola*, between the places of entry of the ducts, but more, as far as could be determined, than in *C. ophiorhysis* (figs. 12 and 14). The difference in size of the spermiducal glands of the two species of *Ceratodrilus* has been commented upon above. *Cambarincola* and *Pterodrilus* have spermiducal glands most nearly like that of *Ceratodrilus* among the genera of branchiobdellids which are well known.

Prostate: The prostate of both species of *Ceratodrilus* is reduced to nothing other than the prostatic bulb. That of *C. ophiorhysis*, however, is more apparent in whole mounts (fig. 14); while that of *C. thysanosomus* frequently cannot be seen at all in such preparations (fig. 12). The prostatic bulb consists of flattened epithelial cells that, from their appearance in hematoxylin-eosin stained sections, may well be muscular (fig. 10). The cavity of the bulb communicates directly by a very narrow, hardly perceptible, lumen which is filled with a secretion, with the lumen of the spermiducal gland. A prostate in developed form is found in the genera *Cambarincola* and *Pterodrilus.* The prostatic bulb is found in some species of *Cambarincola.* In both these genera the prostate, lying closely applied to the spermiducal gland and enclosed with it by the peritoneal covering, opens into the lumen of the spermiducal gland at the point where it becomes muscular to form the ejaculatory duct.

Ejaculatory duct: Histologically, the ejaculatory duct resembles that of other branchiobdellids in which it occurs (Holt, 1949:542, 553). It is, however, relatively prominent in *Ceratodrilus* (figs. 12 and 14) and the lumen is distinct. This structure is called the muscular sperm sac by Moore (1895:521) and is apparently not distinguished from the penial sheath by many authors who call all parts of the male reproductive system ectad to the deferent ducts the atrium. It is known to be absent in *Xirondrilus* and in some species of *Branchiobdella.*

Bursa: The atrial part of the bursa is fairly large in *Ceratodrilus* (table 3) and as always consists of an invagination of the body wall. It is subspherical in shape (figs. 12 and 14) and is eversible (fig. 7). The inner edge of the inwardly projecting layer of epitheliomuscular lining epidermis of the withdrawn atrium (fig. 3) becomes the outer rim of the cup-like, everted atrium (fig. 7). The muscles of the atrium proper are primarily circular with reference to the organ itself, although the organ is so heavily muscular and the muscle fibers are so hard to trace, that the presence of radial muscles, at least, is not ruled out. The penis projects into the ental portion of the cavity of the atrium. In short, the atrium of *Ceratodrilus* is much like that of other branchiobdellids.

The penial sheath is limited entally by the narrowing of the ejaculatory duct and the beginning of a covering of longitudinal (in reference to the organ itself) muscle fibers. Ectally, the penial sheath ends at the point where the circular muscles of the atrium and the longitudinal ones of the sheath are joined. In *Ceratodrilus* there is a distinct outer indentation at this point; in other words, the penial sheath is less in diameter than the atrium (figs. 12 and 14). The penial sheath is composed of two muscle layers, the outer longitudinal one mentioned and an inner circular layer which may be derived from that of the atrium, but which are continuous with the muscle layer of the ejaculatory duct. This inner layer of muscle cells forms strands which traverse the space between the sheath and the penis and attach to the latter, serving, one supposes, to withdraw the penis (figs. 3 and 6).

The penis is a continuation of the lining epithelium of the ejaculatory duct and when completely withdrawn into the penial sheath is folded several times in the ectal part of the sheath (fig. 6), but may be completely everted to form a rather membranous structure somewhat expanded at the outer end (fig. 7).

Whether the eversible penis of *Cirrodrilus* is like that of *Ceratodrilus* cannot be determined without a direct comparison, but Yamaguchi's figure (1934:195) shows the bursa and penis of *Stephanodrilus* [= *Cirrodrilus inukaii*] to be rather like that of *Ceratodrilus* except for the shortness of the penial sheath which is simply the ental part of the atrium.

THE FEMALE REPRODUCTIVE SYSTEM. As remarked above, the female reproductive system proper of *Ceratodrilus* is not noticeably different from that of other branchiobdellids.

SPERMATHECA. The spermatheca of *Ceratodrilus* is a large organ. The bursal part consists of an inturning of the body wall to form a narrow canal of no great extent (fig. 8) lined with an epidermis continuous with and similar to that of the body wall. The spermathecal duct, which is narrow in such species as *Cambarincola macrodonta* Ellis (Holt and Hoffman, 1959: 101), is quite thick in *Ceratodrilus* and constitutes roughly half the length of the entire organ. It is lined with very tall glandular cells whose outer ends, which project into the lumen of the duct, are separated from each other. The nuclei of all these cells are located basally. This part of the spermatheca is enclosed by two muscle layers; an outer circular one and an inner longitudinal one. The spermathecal duct passes over into the spermathecal bulb without any increase in diameter of the bulb over the duct part of the organ (table 3); indeed in *C. thysanosomus* the bulb seems to be slightly less in total diameter than the duct, while the reverse may be true for *C. ophiorhysis*. The great increase in the diameter of the lumen of the bulb is accounted for by the absence of the longitudinal layer of muscles, the reduction in size of the outer circular muscle cells and the great decrease in the height of the cells of the lining epithelium which here are flattened (fig. 8). Generally the lining epithelium of the spermathecal bulb appears to be simply that of a lining epithelium, but in one specimen of *C. thysanosomus* these cells appear glandular, produce clear globules of what may be a secretory material at their free borders and are ciliated (fig 5). Apparently, this represents some sort of physiologically distinct phase in the activity of the spermatheca, since this condition was not observed in other individuals.

Entally, the spermatheca ends in a process in which no spermatozoa are found. The apparent length of this process is variable, but it is always present and the lining epithelium is of a different character from that of the bulb; the cells of this region are composed of a denser and darker staining cytoplasm. Frequently, the process is invaginated at its ental end (fig. 8) and that of *C. thysanosomus* may be slightly longer than that of *C. ophiorhysis*.

There are no specific differences which are clearly constant between the spermathecae of the species of *Ceratodrilus*. The organ is generally similar to that of other branchiobdellids, but differs in the diameter of the spermathecal stalk from that of *Cambarincola* and the ental process is not common in the genera known to the writer.

Much remains to be learned about *Ceratodrilus*. Many more collections are needed from the Snake River basin and nearby regions. Nothing is known of the ecology of the animals. Much more study of the range of morphological variability of *C. thysanosomus* should be done and its distribution in the relict streams of the Great Basin studied in detail. It is hoped that this report of what is known about this interesting genus will encourage workers with a ready access to these regions to investigate some of these problems.

SUMMARY

The history of previous treatments of the genus is reviewed and Hall's generic name, *Ceratodrilus*, is revived. *Ceratodrilus* is separated from *Cirrodrilus* Pierantoni by the presence of four instead of eight peristomial tentacles; by the presence of a prostate in the form of a prostatic bulb; by the deferent ducts entering the spermiducal gland at its ental end instead of along the midlength of the organ; by the absence of a median duct of the spermatheca; and by the presence of a common opening instead of paired ones of the anterior nephridia. A revised diagnosis of *C. thysanosomus* Hall and a diagnosis of *C. ophiorhysis*, n. sp., are presented and compared. The anatomy of the genus is discussed with particular emphasis placed on characters which vary from one group of branchiobdellids to another. Terms applicable to the branchiobdellid reproductive systems are defined and some new ones introduced.

LITERATURE CITED

Ellis, Max M. 1912. A new discodrilid worm from Colorado. Proc. U. S. Nat. Mus. 42: 481-486.

Goodnight, C. J. 1940. The Branchiobdellidae of North American crayfishes. Ill. Biol. Monogr. 17(3): 1-71.

Hall, M. C. 1914. Description of a new genus and species of the discodrilid worms. Proc. U. S. Nat. Mus. 48: 187-193.

Holt, P. C. 1949. A comparative study of the reproductive systems of *Xironogiton instabilius instabilius* (Moore) and *Cambarincola philadelphica* (Leidy) (Annelida, Oligochaeta, Branchiobdellidae). Jour. Morph. 84(3): 535-572.

———. 1953. Characters of systematic importance in the family *Branchiobdellidae* (Oligochaeta). Va. Jour. Sci., 4(2): 57-61.

———. 1955. A new branchiobdellid of the genus *Cambarincola* (Oligochaeta, Branchiobdellidae) from Kentucky. Jour. Tenn. Acad. Sci. 30(1): 27-31.

———. and R. L. Hoffman. 1959. An emended description of *Cambarincola macrodonta* Ellis with remarks on the diagnostic characters of the genus (Oligochaeta, Branchiobdellidae). Jour. Tenn. Acad. Sci. 34(2): 97-104.

Moore, J. P. 1894. On some leech-like parasites of American crayfish. Proc. Acad. Nat. Sci. Phila. 45(for 1893): 419-428.

———. 1895. The anatomy of *Bdellodrilus illuminatus,* an American discodrilid. Jour. Morph. 10: 497-540.

Pierantoni, V. 1905. *Cirrodrilus cirratus,* n.g.n.sp. Parasita dell' Astacus japonicus. Ann. Mus. Zool. Univ. Napoli. N. S. 1(31).

———. 1906. 2 nuovi discordridi del Giappone e della California. Ann. Mus. Zool. Univ. Napoli. N. S. 2(11).

———. 1912. Monografia dei Discordrilidae. Ann. Mus. Zool. Univ. Napoli. N.S. 3(24).

Stephenson, J. 1930. The Oligochaeta. Oxford.

Yamaguchi. H. 1932a. On the genus *Cirrodrilus* Pierantoni, 1905, with a description of new *Branchiobdella* from Japan. Ann. Zool. Japan. 13(4): 361-367.

———. 1932b. Description of a new branchiobdellid, *Carcinodrilus nipponicus,* n.g.n.sp. Jour. Fac. Sci. Hokkaido Imp. Univ. 2(ser. 6) (1): 61-67.

———. 1932c. A new species of *Cambarincola,* with remarks on spermatic vesicles of some branchiobdellid worms. Proc. Imp. Acad. 8(9): 454-456.

———. 1933. Description of a new branchiobdellid, *Cambarincola okadai* n. sp., parasitic on American crayfish transferred into a Japanese Lake. Proc. Imp. Acad. 9(4): 191-193.

———————. 1934. Studies on Japanese Branchiobdellidae with some revisions on the classification. Jour. Fac. Sci. Hokkaido Imp. Univ. 3 (ser. 6) (3): 177-219.

EXPLANATION OF PLATES

All figures, except fig. 1, which is adapted from Yamaguchi (1934: 194) and fig. 2, were drawn with the aid of a camera lucida.

Legend. — *a,* atrium; *b,* bursa; *cp,* cephalic tentacles; *dd,* deferent duct; *ejd,* ejaculatory duct; *enp,* ental process of spermatheca; *esg,* lining epithelium of spermiducal gland; *j,* jaw; *jn,* junction of nephridial outlet ducts; *np,* nephridiopore; *op,* oral papillae; *p,* penis; *pb,* prostatic bulb; *ps,* penial sheath; *sb,* spermathecal bulb; *sd,* spermathecal duct; *sg,* spermiducal gland; *spb,* spermathecal bursa.

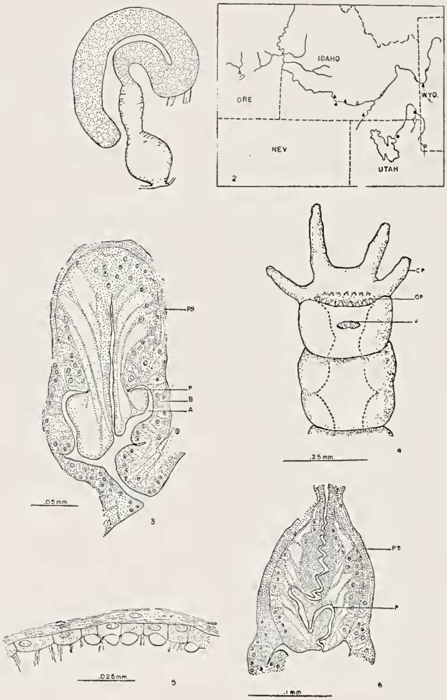
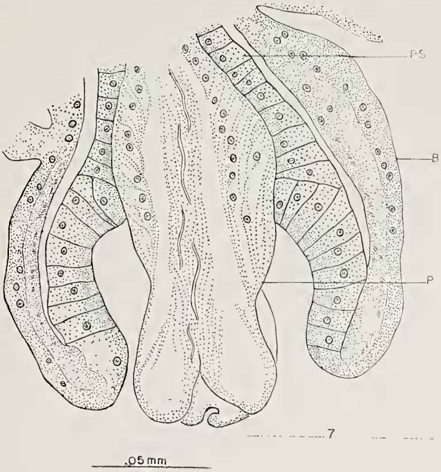


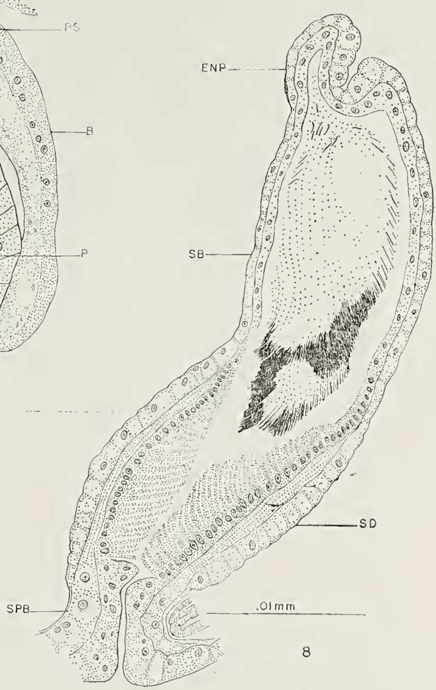
Plate I

Explanation of Figures

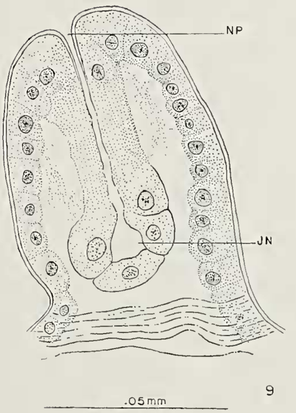
1. Male deferent apparatus of *Stephanodrilus inukaii,* after Yamaguchi (1934:194).
2. Distribution of *Ceratodrilus.* Circles indicate records for *C. thysanosomus;* triangles records for *C. ophiorhysis.* Solid figures indicate Holt's records; open ones, Goodnight's.
3. Oblique section of penial sheath, penis and atrium of *C. ophiorhysis.*
4. Ventral view of head of *C. ophiorhysis.*
5. Portion of wall of spermathecal bulb of *C. thysanosomus.*
6. Longitudinal section of penial sheath and penis of *C. thysanosomus.*



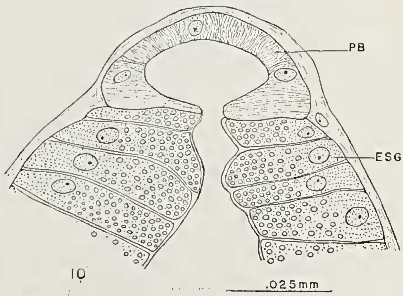
7



8



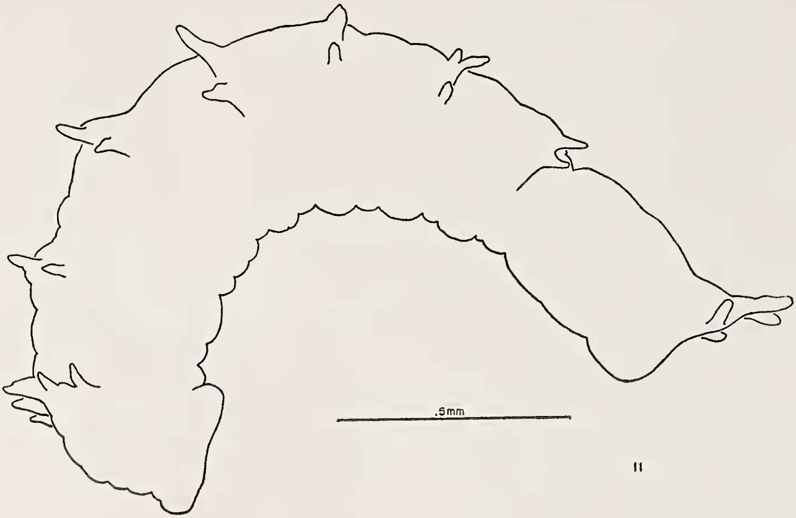
9



10

Plate II

7. Longitudinal section of everted bursa and penis of *C. thysanosomus*.
8. Longitudinal section of spermatheca of *C. ophiorhysis*.
9. Longitudinal section through the nephridiopore of *C. thysanosomus*.
10. Section through prostatic bulb and portion of spermiducal gland of *C. ophiorhysis*.



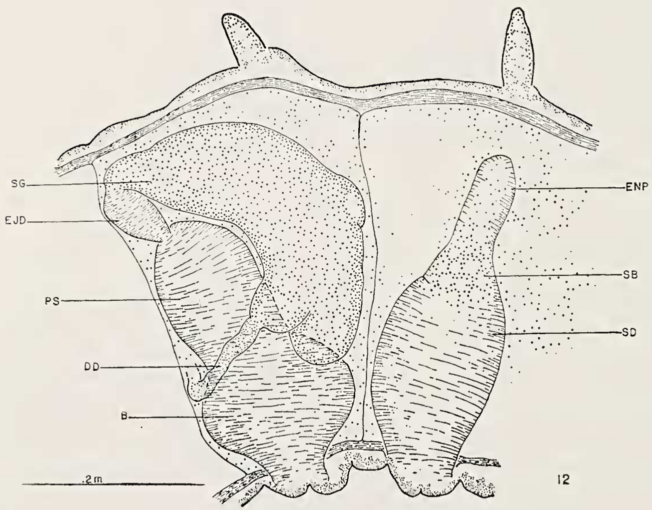


Plate III

11. Outline drawing of *C. thysanosomus.*
12. Lateral view of reproductive organs in segments v and vi of *C. thysanosomus.*

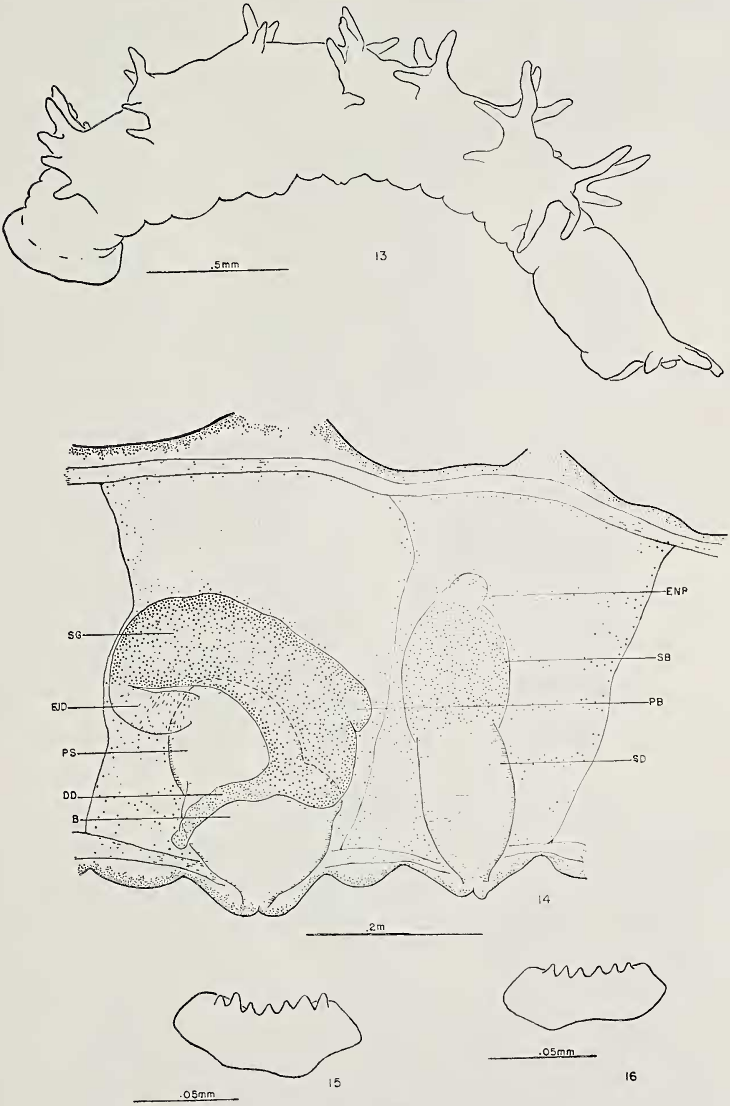


Plate IV

13. Outline drawing of *C. ophiorhysis*.
14. Lateral view of reproductive organs of *C. ophiorhysis*.
15. Upper jaw of *C. ophiorhysis*.
16. Lower jaw of *C. ophiorhysis*.